A new brush-finch in the *Atlapetes latinuchus* complex from the Yariguíes Mountains and adjacent Eastern Andes of Colombia

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The brush-finches *Atlapetes* are Neotropical passerines which achieve greatest diversity in the Andes and whose taxonomy and ecology have received much recent attention. *Atlapetes* shows a high degree of geographical variation, with various forms restricted to particular elevations, mountains or slopes, but few cases of true sympatry. The group is therefore ideally suited to studies of the patterns and mechanisms of speciation (Remsen & Graves 1995a, García-Moreno & Fjeldså 1999). Even recently, localised taxa have been described, both at species and subspecies level (e.g. Fitzpatrick 1980, Remsen 1993, Valqui & Fjeldså 1999), and a species thought possibly extinct was rediscovered (Agreda *et al.* 1999).

Serranía de los Yariguíes and the Eastern Cordillera

The Eastern Cordillera (Eastern Andes) is one of Colombia's three principal mountain ranges, extending from dpto. Cauca (01°N), to the Serranía de Perijá, on the Caribbean coast (11°N). It is characterised by a varied habitats, with slopes bordering Amazonia, the llanos and Magdalena Valley, humid and dry regions, plateaux, steep slopes and wetlands. The cordillera's cool climate and high-elevation savannas have long been subject to human development. It is also one of the world's major centres of avian endemism, the Colombian East Andes Endemic Bird Area (Stattersfield *et al.* 1998).

The Serranía de los Yariguíes (dpto. Santander) is an isolated western spur of the East Andes, rising to *c.*3,400 m and isolated from the rest of the cordillera to the north and east by the Sogamoso Valley, and to a lesser extent to the south by depressions associated with the ríos Horta, Quirola and Opón and their tributaries. A collection of 60 bird species was made below 1,000 m near San Vicente de Chucurí in November 1956 (Borrero & Hernández 1957), and a few specimens were taken elsewhere on the massif, generally on the drier eastern slope (e.g. Romero 1983), but the humid western slope and highest elevations were very poorly known ornithologically prior to our field work (for general results see Donegan & Briceño 2005, Donegan & Huertas 2005, Donegan & Avendaño 2006, Huertas & Donegan 2006). Amongst the birds we recorded was one which initially appeared to be of the 'Northern Rufous-naped Brush-finch' or 'Yellow-breasted Brush-finch' complex, *A. latinuchus*.

Paynter (1978) specifically commented on the absence of records of *A. latinuchus* (then classified as *A. rufinucha*) from the central part of the Eastern Cordillera, noting 'While it is present in the Sierra de Perijá, a northward extension

of the Eastern Andes on the Venezuela–Colombia border, it has not been found in the Eastern Andes except for a few dubious records from Bogotá (*A. r. simplex*, known only from native Bogotá specimens)'. The range of *A. l. simplex* was subsequently thought to comprise the central eastern plateaux and perhaps the east slope of the Eastern Andes between Lago de Fuquene (dpto. Cundinamarca) and Soatá (dpto. Boyacá) (Borrero & Olivares 1955, Hilty & Brown 1986, Ridgely & Tudor 1989). However, such records and reported 'variations' in the plumage of *A. l. simplex* derive from immatures and subadults in collections, a failure to compare types and new material, and the existence of two taxa from different regions.

Methods

The Colombian EBA (Evaluation of Biodiversity in the Andes) Project is an ongoing research and conservation initiative, supported by Fundación ProAves, that has conducted Rapid Biodiversity Assessments of remote and/or unstudied sites since the mid 1990s.

We studied ten primary-forest sites on both slopes of the Serranía de los Yariguíes at elevations of 100–3,200 m between January 2003 and January 2006. Each site was subject to 4–6 days' field work using mist-netting (up to 220 m of mist-nets) and non-systematic observations including sound-recording and playback. On 4–8 January 2004, we visited a remote site, at 2,400–2,450 m, on the west slope, accessed from Cantagallos, in San Vicente de Chucurí municipality, to Finca Santo Domingo (2,250 m), from where we reopened a disused trail to the ridge at 2,450 m.

On 6 January 2004, together with Elkin Briceño, we trapped an *Atlapetes* which showed features of the *A. latinuchus* complex, e.g. a rufous cap, black mask, yellow underparts and an indistinct moustachial (Fig. 1A–B), but differed from all other populations in its jet black mantle, tail and wings, and from some taxa in the group by the lack of a white speculum. *A. latinuchus* is unknown from the north-central Eastern Cordillera (Hilty & Brown 1986), with the distinctive form *A. l. nigrifrons* to the north and paler-backed *A. l. simplex* postulated to occur further south in the cordillera. Given this, we considered it probable that the bird represented an undescribed taxon. Due to poor weather conditions for photography, we retained the bird overnight for further study but, unusually for an *Atlapetes*, it died overnight. The bird was prepared in the field as a flat skin.

Comparison of our photographs and wing- and tail-feathers from the bird with a 'Bogotá' *A. l. simplex* in the Natural History Museum (NHM; Tring) revealed various differences between them, with *A. l. simplex* having a grey/brown back, paler red crown, small white speculum and larger yellow supraloral spot (Fig. 1C). Further research revealed additional specimens of the black-backed form from the Virolín area, dpto. Santander, on the west slope of the main Eastern Cordillera, *c.*60 km south-east of Serranía de los Yariguíes. On 8 January 2005, at Lepipuerto, on the upper río Chimera, El Carmen/Simacota municipality (06°28'N, 73°28'W; 2,900 m), TD and Martin Donegan observed and sound-recorded a pair foraging in

Figures 1A–B. Holotype of *A. l. yariguierum* (Blanca Huertas/EBA Project)

Figure 1C. *A. l. simplex* (=*A. l. spodionotus*) neotype (Thomas Donegan, © Natural History Museum, Tring). Note difference in contrast between upperparts and mask colour compared to the holotype, the very small but visible white speculum and relatively strong malar, each consistent with *A. l. spodionotus*.

páramo. Further observations and the capture of another bird (from which a blood sample was obtained) were made in July 2005, during 'Proyecto YARE', by ourselves and Jorge Avendaño in páramo at Filo Pamplona, Galán municipality (06°38'N, 73°24'W; 3,200 m), on the east slope of the massif.

Type material of *A. l. simplex*

Project Biomap provided data from all museums holding Colombian specimens. We also searched an online database (www.biologie.uni-ulm.de) of all major German museums, but were unable to locate the two *A. l. simplex* specimens mentioned in the type description (Berlepsch 1888). All remaining specimens from the Berlepsch collection are now held in Frankfurt, except a few specimens in Warsaw (F. Steinheimer *in litt.* 2005), neither of which institutions possess any *A. l. simplex*

Figure 1D. Close-up of mantles and crown of (left to right) adult *A. l. simplex* neotype ('Bogotá', Colombia = *A. l. spodionotus*), subadult *A. l. elaeoprorus* (Central Andes, Antioquia, Colombia), adult *A. l. comptus* (southern Ecuador and northern Peru), and adult *A. l. spodionotus* (Ecuador and southern Colombia). (Thomas Donegan, © Natural History Museum, Tring). Note contrast between the grey upperparts and black face on *A. l. simplex* compared with much darker *A. l. elaeoprorus*, and the paler crown of *A. l. simplex* compared to *A. l. elaeoprorus*. *A. l. yariguierum* averages blacker than *A. l. elaeoprorus* with essentially no contrast between the mask and upperparts in adults. Note also similarity between '*A. l. simplex*' and *A. l. spodionotus*. NB: adult male *A. l. elaeoprorus* has essentially black upperparts (as in tail of the subadult), not black admixed olive.

(G. Mayr *in litt.* 2005, N. Krabbe *in litt.* 2006). It seems probable that the *A. l. simplex* types were either destroyed or lost during World War II (G. Mayr *in litt.* 2005). The *A. l. simplex* at NHM is a male, apparently adult, originally from the Berlepsch collection. It too is dated 1888, and the label is annotated 'agrees with types' in Berlepsch's hand. The plumage, particularly the trace of a small white speculum, is consistent with Berlepsch's (1888) brief description (although some apparent adult/immature variation is noted, with the adult somewhat darker). This specimen, like the types, is labelled 'Bogotá'. Thus, we assume this specimen to be typical of the form described by Berlepsch as *A. l. simplex*, and propose to treat it as a neotype of *A. l. simplex*.

A. l. simplex is a junior synonym of *A. l. spodionotus*

The *A. l. simplex* neotype is indistinguishable from *A. l. spodionotus* of the main Andean range in southern Colombia and northern Ecuador. 'Bogotá' trade skins originated from as far away as Panama or Ecuador and several taxa (including the recently described Bogotá Sunangel *Heliangelus zusii*) are known only from such material (see Graves 1993). *A. l. simplex* was described with, and appeared in the same consignment as, the antbird taxon *Myrmeciza longipes boucardi*, a form now known to be restricted the upper Magdalena Valley of Colombia, from dpto. Tolima to the headwaters at 1,700 m (Hilty & Brown 1986). It seems feasible that *A. l. simplex* skins may originate from slightly further south, where *A. l. spodionotus* is present. Other taxa until recently known in Colombia only or principally from Bogotá skins, e.g. Band-bellied Owl *Pulsatrix melanota*, Black-streaked Puffbird *Malacoptila fulvogularis* and Red-billed Parrot *Pionus sordidus*, have recently been found there (Salaman *et al.* 2002). The case for *A. l. simplex* being distinct from *A. l. spodionotus* was not made by Berlepsch (1888), who focused on the differences from *A. l. elaeoprorus* of Antioquia. It seems that *A. l. simplex* is better treated as a junior synonym of *A. l. spodionotus* (Sclater & Salvin 1879).

Description

With the status of *A. l. simplex* resolved, questions concerning the dark-backed populations of *A. latinuchus* in the Serranía de los Yariguíes and adjacent slope of the Eastern Cordillera is clarified, and some supposed 'variations' in plumage of birds from this region can be discarded. This Eastern Cordillera population differs from all other described *Atlapetes* taxa. We propose to name it:

***Atlapetes latinuchus yariguierum* subsp. nov.**
Yariguíes Brush-finch
Gorrión-montés de los Yariguíes

Holotype Adult male, no. ICN-34016 of the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), Bogotá, Colombia (Fig. 1a). Prepared by TD, on 7 January 2004, at Alto Cantagallos,

Serranía de los Yariguíes, San Vicente de Chucurí municipality, dpto. Santander, Colombia (06°49'N, 73°22'W). Study specimen produced from flat skin by F. G. Stiles. The locality is at 2,400 m on the west slope of the Yariguíes massif, Eastern Andes, in lower montane cloud forest. Tissue samples and stomach contents are held at the Instituto Alexander von Humboldt's molecular laboratory, Cali, Colombia.

Paratypes and other material We examined specimens of all *A. latinuchus* taxa (except *A. l. chugurensis*) in the following institutions: ICN (Bogotá), NHM (Tring), University Museum of Zoology, Cambridge, UK (UMZC), Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH), Museo de la Universidad de la Salle, Bogotá, Colombia (MLS), Museo de Historia Natural, Universidad Industrial de Santander, Bucaramanga, Colombia (UIS) and Muséum National d'Histoire Naturelle, Paris, France (MNHN). Digital photographs of all *A. latinuchus* specimens in the Colección Ornitológica Phelps, Caracas, Venezuela (COP) and some in the Field Museum of Natural History, Chicago, USA (FMNH) were also inspected (see Appendix 1). We assign the following paratypes:

Adult sex unknown, no. UIS 1412, collected by V. H. Serrano, on 23 August 2001, at Santa Helena (06°00'N, 73°09'W), between Charalá and Duitama, Boyacá, at 2,400 m, on the west slope of the Eastern Andes. Subadult female, no. ICN-25111, prepared 28 November 1978 (collector unknown), from Charalá, dpto. Santander (*c*.06°05'N, 73°12'W) on the west slope of the Eastern Andes. Subadult (probably female), DNA sample and photographs taken on 12 July 2005 by TMD & J. Avendaño, at Filo Pamplona, Serranía de los Yariguíes (06°38'N, 73°24'W; 3,200 m); DNA sample deposited at UIS.

The following juveniles also appear to be of the new taxon but are not assigned as paratypes: juvenile male, no. ICN-3199, collected by A. Olivares, on 7 January 1953, at Soatá, Alto de Onzaga, Boyacá, (*c*.06°35'N, 72°07'W) on the east slope of the East Andes (juvenile plumages are poorly known, making this is a tentative identification); juvenile of unknown sex, no. ICN-10322, collected by A. Olivares & P. Bernal, on 9 July 1961, in Vereda Ruparita, 2 km east of Arcabuco, Boyacá, (*c*.05°73'N, 73°45'W) on the west slope of the East Andes.

The following specimens, of which we have seen digital photographs, are also apparently of the new taxon but are not assigned as paratypes: subadult male, no. FMNH-220606, collected by Kjell von Sneidern, in 1950, above Chiquinqirá, Boyacá (*c*.05°37'N, 73°50'W) on the east slope of the East Andes; juvenile. no. FMNH-220607, taken by the same collectors, from the same locality, on the same date as ICN-10322.

Diagnosis A typical *Atlapetes* with various characteristics of the *A. latinuchus* complex, including dark upperparts and yellow underparts, a rufous crown, (concealed) white speculum, black mask and indistinct moustachial (Hilty & Brown 1986), but differing from others within the *A. rufinucha* complex by its sharply demarcated rufous cap (at least in adults), yellow malar, slight melanism on the

flanks, and white speculum (García-Moreno & Fjeldså 1999). Analysis of molecular data shows it to be related to *A. l. elaeoprorus* and *A. l. spodionotus* (see below).

A. l. yariguierum differs from all forms of *A. latinuchus* in its uniform jet black mantle, tail, and wings (with no olivaceous or greyish tones, except in juveniles, or white speculum), and virtually no contrast between the black mask and upperparts (though some adult *A. l. elaeoprorus* approach this). A 'rather greyish back' was considered diagnostic of the *A. latinuchus* group by García-Moreno & Fjeldså (1999). Adult *A. l. yariguierum* is notably darker rufous on the crown than other *A. latinuchus* taxa (some adult *A. l. elaeoprorus* approach it), and is further distinguished by the lack of a visible speculum, obvious supraloral spot, dark forehead markings, strong malar or white/cream on the nape. Similarities between *A. l. elaeoprorus* and *A. l. yariguierum* perhaps indicate previous contact between taxa of the northern Central and Eastern Cordilleras, also evidenced amongst subspecies of *Grallaricula nana*, *Phaethornis syrmatophorus* and *Basileuterus*

Figure 2. From left to right (youngest to oldest): juvenile apparent *A. l. yariguierum* (Soatá, Boyacá, east slope of East Andes); juvenile *A. l. yariguierum* (Arcabuco, Boyacá, west slope of East Andes); subadult paratype *A. l. yariguierum* (Virolín, Santander, Colombia, west slope of East Andes), and adult holotype *A. l. yariguierum* (Serranía de los Yariguíes, Santander, Colombia) at ICN-UN (Thomas Donegan). Note black tails of all birds. Ages ascribed on basis of plumage as no skull ossification data on specimen labels (except holotype).

tristriatus (TMD unpubl.). However, *A. l. elaeoprorus* always has a large white speculum and large yellow supraloral (unlike the almost indiscernible short line of yellow feathers below the rufous cap in *A. l. yariguierum*). Juvenile *A. l. elaeoprorus* has the back tinged dark greenish, whereas in *A. l. yariguierum* it is tinged dark brownish.

A. l. yariguierum differs from *A. l. spodionotus* in its combination of black mantle and tail, deeper rufous crown and reduced yellow feathering at the bill base. A report of the supraloral being variable in *A. l. simplex* (Paynter 1978) appears based on differences between the types and recent Eastern Cordillera material. Some *A. l. spodionotus* (including the *A. l. simplex* in Tring) show traces of a visible speculum in the folded wing. In all *A. l. yariguierum* observed in the field or museum, the speculum is invisible on the folded wing, though this feature could be visible, especially when moulting. In *A. l. spodionotus*, where the speculum extends almost to the greater coverts, it is visible in some individuals and not in others (Paynter 1978).

A. l. yariguierum is separable from the *A. schistaceus* group by its yellow underparts and lack of strong moustachial or supraloral; from *A. albofrenatus* taxa by the absence of a well-defined moustachial and its black (not olive-green) mantle; from *A. l. nigrifrons* and *A. melanocephalus* by the lack of a black upper throat or forehead, pale moustachial or grey lores, and from the latter by its rufous cap; and from *A. pallidinucha* taxa in its uniform dark rufous crown and nape in adults. Morphometrics of these taxa are presented in Appendix 3.

Description of holotype Capitalised colour nomenclature and numbers from Munsell Color (1977) and Munsell Color (2000). Adult male with skull 100% ossified (mass 22.6 g). Testes 8 mm × 5 mm (apparently somewhat enlarged with small cloacal protuberance in life) and little subcutaneous fat. Stomach contents included various small pieces of Coleoptera exoskeleton. Twelve rectrices, nine primaries, six secondaries and three tertials, typical of the Emberizinae. Flight-feathers fresh, with rectrices full (except fifth rectrix from left, 95% emerged), suggesting recent completion of moult. Emarginated pp6–9 (slight emargination on p5), with rounded wing point pp4–6 and primary notches absent (following Proctor & Lynch 1993). Max. flattened wing (following Svensson 1992) 77 mm, tail 80 mm, tarsus 25 mm, culmen to skull 16 mm. Crown dark rufous (closest to P, 10R: 4/8); facial mask jet black; mantle, wing-coverts, alula, flight-feathers, rump and rectrices closest to black (Gley 1: 2.5/2.5 but darker; *cf.* greyish brown, closest to 10YR 3/1 or 2/2 of '*A. l. simplex*' and *A. l. spodionotus*), with virtually no contrast between mask and back. Very narrow line of six short Yellow (5Y 8/12) feathers below rufous crown, at base of bill. Throat, malar, breast and belly uniform Yellow (5Y 8/12), becoming slightly yellower on belly and washed slightly darker on flanks. Indistinct darkish moustachial extends *c.*16 mm from bill. Underside of carpal Yellow (5Y 8/12) with small blackish spots. Base of pp4–6 concealed under greater coverts frontally White (Gley 1 8/1). Each except outermost primary and innermost

five secondaries distally near White (Gley 1 8/1). Bare parts: mandible uniform black; legs horn, with feet soles yellowish grey; iris dark rufous.

Variation in the series Plumage and biometrics of the adult paratype essentially very similar to those of the holotype. The subadult paratype at UIS has a slightly paler rufous cap (*c.*2.5YR 4/8, but still darker than adult *A. l. simplex/spodionotus*),

Figure 3. Map showing sites at which *A. l. yariguierum* has been reported (blue squares; unfilled squares = unconfirmed records). All *A. l. yariguierum* records post-date Paynter (1972). Also shown are known ranges of *A. l. elaeoprorus* (unfilled red circles); *A. l. caucae* (purple-filled circles); and *A. l. spodionotus* (unfilled pink ellipses) in Colombia, based on specimens, published literature, data from Project Biomap and additional sight records reported to the authors. Apparent gaps in distribution are partly due to observational lacunae, sometimes exacerbated by deforestation, and partly due to ranges of congeneric ecological competitors (see Remsen & Graves 1995). The southernmost record of *A. l. elaeoprorus* in the West Andes and the northernmost, from the Serranía de San Lucas, are from data supplied by Project Biomap. Both require confirmation. Observations from the East Andes in Cauca are of birds with a strong white speculum (J. Idrobo *in litt.* 2005) and therefore appear more likely to be of *A. l. caucae* than *A. l. spodionotus*. Of this group, *A. l. yariguierum* emerges as the taxon known from the largest number of localities in Colombia.

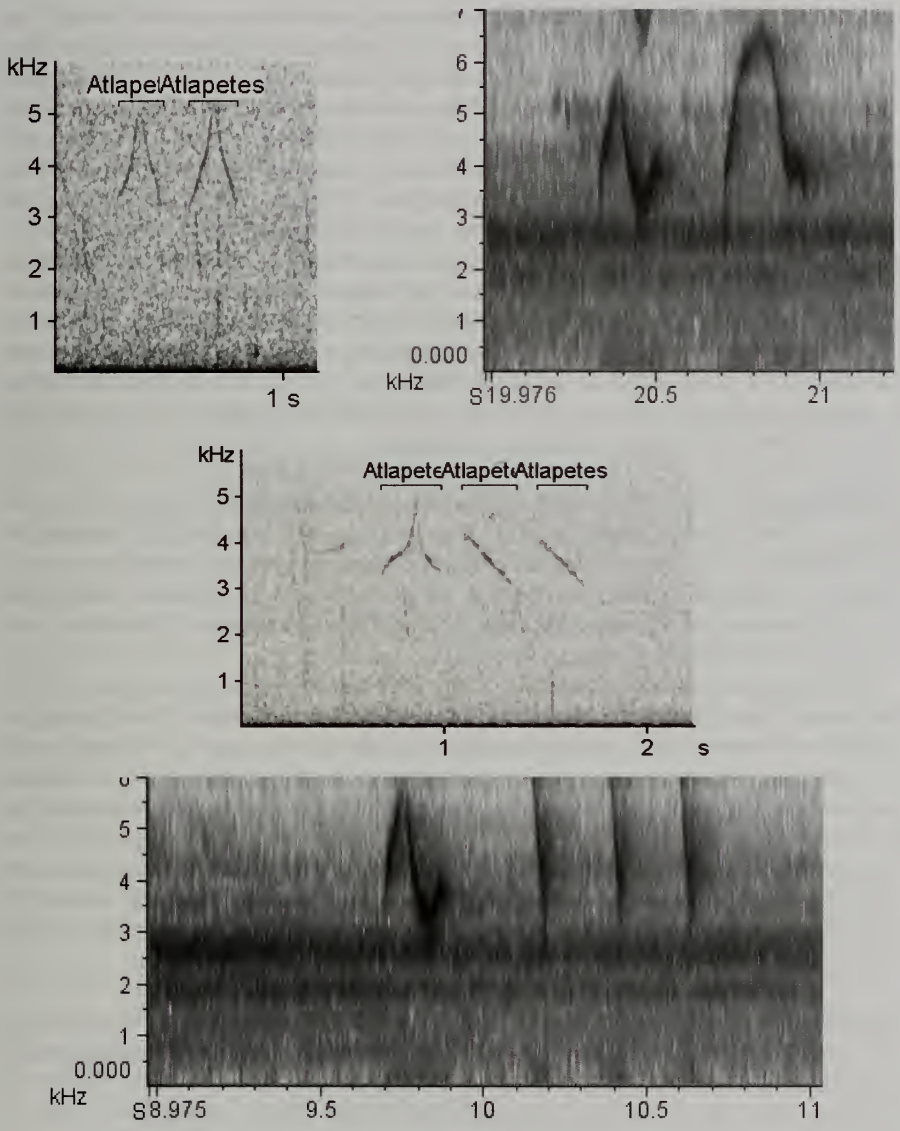

Figure 4. Vocalisations of *A. l. yariguierum* recorded at Lepipuerto, Serranía de los Yariguíes (top left and middle). Sonograms of *A. l. yariguierum* produced by Richard Ranft (British Library) using Avisoft Pro software from recordings by TMD. In each case, *A. l. yariguierum* vocalisations are presented together with the most similar recordings of *A. l. spodionotus* from Yanacocha, Pichincha, Ecuador (00°08'S, 78°35'W). Sonograms for *A. l. spodionotus* were produced by TMD using Raven Lite software, from recordings by J. V. Moore *in* Krabbe *et al.* (2001).

both black and brownish (particularly at the base of the rump) mantle feathers, but the tail- and flight-feathers and most of the upperparts similar to adults. The demarcation between the rufous crown and dark back is less sharp in non-adults of *A. l. yariguierum*, a feature of other *A. latinuchus* taxa (birds in Vellinga *et al.* 2004 are probably an example of this). ICN-3199 is similar to the subadult paratype, but has more brownish and fewer black feathers, a paler crown and less obvious demarcation between the crown and upperparts. It has a very pale rufous nape (approaching *A. pallidinucha*) and more brown and fewer black feathers in the upperparts. The juvenile at FMNH has a darker crown and nape but similar upperparts. All specimens in the series have a jet black tail (as does *A. l. elaeoprorus* at all ages). The ICN series appears in Fig. 2. We cannot eliminate the possibility that *A. l. yariguierum* may involve two taxa or clinal variation: it seems feasible that those from Yariguíes are on average slightly darker overall with less yellow on the supraloral than birds from the main cordillera. The pale-naped bird from the east slope in Soatá also requires further investigation.

Vocalisations We sound-recorded a pair observed at Lepipuerto (Fig. 4). The call is typical of the genus: a short series of high-pitched, rising and falling whistles at *c.*3–5 kHz: *wiu-wiu*, *wiu-weeu-weeu*, *wee-weeu-weeu* and *wee-wiu-weeu-weeeu*. TD also once heard a 'stuttering' finch song, probably *A. l. yariguierum* and similar to *A. latinuchus* in Ecuador, but this was not sound-recorded. Recordings are deposited at the British Library (no. 142861), London.

Published sound-recordings of *A. l. spodionotus* from Ecuador suggest that *A. latinuchus* taxa, like other oscines, possess a wide repertoire. Small possible differences between *A. l. spodionotus* and *A. l. yariguierum* are: *A. l. yariguierum* calls appear simpler and include notes that increase and decrease in pitch more uniformly (straight line on the sonogram), and which decrease in pitch more slowly, than in *A. l. spodionotus*. With just two recordings of *A. l. yariguierum*, it is impossible to know whether calls are significantly different from *A. l. spodionotus*, which has very varied calls (Krabbe *et al.* 2001). Vocalisations are poorly known for Colombian *Atlapetes*, begging additional research which may have taxonomic implications.

Distribution It is probable that *A. l. yariguierum* is restricted to high elevations in the Serranía de los Yariguíes and adjacent Eastern Andes (Fig. 3). We are aware of the following records: Galilea, Reserva Biológica Chachalú (06°05'N, 73°09'W; 2,350 m, the paratype locality), trapped 30 October 2003 (weight 30 g) and 27 November de 2003 (weight 28.7 g), with three sight records (D. A. Rincón G.). Rogitama, dpto. Boyacá (*c.*05°47'N, 73°31'W), south-west of Chachalú, where frequently observed and an adult photographed (R. Chavarra C.). Soatá, Boyacá (see Paratypes), in oak forest at *c.*2,900–3,100 m (O. Cortés), El Talisman, Serranía de los Yariguíes (*c.*06°51'N, 73°22'W) photographed in February 2006 at 2,050 m (M. Sharp & C. Turner).

The following records also probably involve *A. l. yariguierum* but require confirmation: Finca El Diviso, dpto. Santander (07°08'N, 73°02'W; 1,850m), on 30 December 2004 (D. A. Rincón G.); Mesa de los Otero, Curití municipality, dpto. Santander (06°37'N, 73°00'W, 2,100–2,250 m), on 19 November 2004 (J. Parra B.); Santuario de Fauna y Flora Iguaque, dpto. Boyacá (05°40'N, 73°27'W, 3,045–3,065 m) (C. D. Cadena & J. E. Zuluaga); and Sutamarchan, Serranía de Merchan, dpto. Boyacá (*c.*05°37'N, 73°38'W), in April 2003 (M. Á. Echeverry).

Overall, a pattern of fairly continuous distribution within humid forests of the central Eastern Andes, principally on the west slope but also apparently on the east side, emerges. To date, *A. l. yariguierum* has been recorded at 1,800–3,200 m, being apparently at least partially replaced lower by Yellow-throated Brush-finch *A. gutturalis* (recorded at 2,000 m on the west slope of Serranía de los Yariguíes) and Moustached Brush-finch *A. albofrenatus* (recorded at 2,000 m on both slopes of Serranía de los Yariguíes). In the main cordillera, it is at least partially replaced at high elevations by Slaty *A. schistaceus* and Pale-naped Brush-finches *A. pallidinucha*, though neither of these has been recorded in the Yariguíes range in surveys almost to the peak, where *A. l. yariguierum* is present. Elevational and latitudinal distributions of these taxa are described and discussed in Remsen & Graves (1995a). The range of *A. l. yariguierum* is shared by other endemics, e.g. Gorgeted Wood-quail *Odontophorus strophium* and Mountain Grackle *Macroagelaius subalaris*, which are both Critically Endangered (BirdLife International 2004).

Etymology Our name honours the Yariguíes indigenous people and the massif that bears their name, expressed as a fifth declension feminine Latin noun *yariguies*, and declined in the genitive plural. Serranía de los Yariguíes is often labelled on maps as Serranía de los Cobardes (Mountains of the cowards), which derives from the colonial era. The Yariguíes people resisted the Spanish, although was doomed to fail in the face of a technologically superior military power. Rather than submit, the Yariguíes committed mass suicide. The Spanish viewed this not as an act of dignity, but of cowardice. Colombian governmental agencies and NGOs are endeavouring to remove the insult from official materials, and Serranía de los Yariguíes is now the preferred name. The region is rich in archaeological sites and indigenous art, which to date have gone largely unrecognised due to the historic security situation and difficulty of access.

Ecology

The holotype was captured in a treefall gap with successional vegetation, *c.*1 km from human-modified habitat, in forest on a west-facing slope overlooking the Magdalena Valley, characterised by a canopy of 8–14 m, dense understorey and epiphytic growth, persistent fog or rain, little insolation (less than 30 minutes daily during field work), and 30–50° slope. Observations at Lepipuerto were made in pristine primary treeline and páramo habitat *c.*30 km from any human population,

and also subject to very high levels of precipitation, with torrential rain lasting several hours each day during the 'dry' season, and frequent ground-level cloud cover. The pair observed here foraged in small tree-like shrubs on an exposed slope. Observations at the third site in Serranía de los Yariguíes were also in pristine treeline and páramo habitat far from human populations. All three sites are within the same tract of forest, this being one of the largest such forests in northern Colombia. Successional primary forest, at the type locality, and fairly open vegetation of the Yariguíes páramo appear to be the natural habitat of *A. l. yariguierum*. *A. latinuchus* taxa regularly invade secondary habitats (Remsen 1993, Hilty, 2003). The new taxon also appears to do so, and indeed seems commoner in such habitats than in primary forest in the main Eastern Andes.

Moult

The very fresh plumage and emergent rectrix of the holotype indicate it had recently completed a moult, whilst the enlarged testes and cloacal protuberance indicate pre-breeding moult, and that this form's breeding season coincides with the wettest part of the year, in February–April (the main breeding season in the adjacent Central Andes of the Magdalena Medio: Cuervo *et al.* 2001).

Discussion

García-Moreno & Fjeldså (1999) recently re-evaluated species limits within *Atlapetes* using molecular data. The taxonomy of the group was previously based on morphological analyses (Paynter 1972, 1978), with the taxa *A. schistaceus* and *A. rufinucha* delimited largely on the presence of grey (*schistaceus* group) or yellow underparts (*rufinucha*; *pileatus* group). Thereafter, Remsen & Graves (1995a) suggested that several geographically close taxa with alternating grey and yellow underparts may be more closely related to one another than to more geographically distant taxa with similar underparts coloration. García-Moreno & Fjeldså's phylogeny supported Remsen & Graves' propositions, and suggested further that many sister taxa should be ranked specifically.

García-Moreno & Fjeldså's analysis concentrated on southern Andean taxa. Their suggestion that the various Bolivian, Peruvian and some Ecuadorian *Atlapetes* be reassigned to two polytypic and six monotypic species has been followed by most subsequent works (Rodner *et al.* 2000, Ridgely & Greenfield 2001, Salaman *et al.* 2001, Hilty 2003, Dickinson 2003, Remsen *et al.* 2006). The northern taxa of *A. latinuchus*, *A. schistaceus*, *A. albofrenatus* and *A. melanocephalus* were not studied in detail, but various taxa formerly considered part of *A. rufinucha*, namely *baroni, caucae*, *chugurensis*, *comptus*, *elaeoprorus*, *latinuchus*, *nigrifrons* (=*phelpsi*: see below), *simplex* (=*spodionotus*) and *spodionotus*, were tentatively reassigned to *A. latinuchus*. García-Moreno & Fjeldså noted 'Our study did not include ... various more richly coloured forms in the northern Andes ... However, it is evident that the current sequence does not reflect natural groupings'.

Due to uncertainties in species limits amongst northern *Atlapetes* taxa and in order to describe *A. l. yariguierum* appropriately, we undertook a preliminary phylogenetic analysis of relevant taxa using a matrix of 16 adult plumage characters. We studied García-Moreno & Fjeldså's 'southern branch', 'central branch' and 'northern branch' taxa (except *A. rufigenis*) together with all other *A. latinuchus*, *A. schistaceus* and *A. tricolor* taxa, as well as *A. fuscoolivaceus*, *A. albofrenatus* and *A. melanocephalus* (which are considered closely related to 'northern branch' species by Paynter 1978), *A. l. yariguierum* and a morphologically distinctive *Atlapetes* recently collected by A. Camero and A. Rodríguez in the Sierra de Perijá ('Perijá bird'). Chestnut-capped Brush-finch *Buarremon brunneinucha* was used as an outgroup to permit comparison with García-Moreno & Fjeldså's phylogeny. Our matrix of character states was compiled from the literature (Paynter 1978, Hilty & Brown 1986, Ridgely & Tudor 1989, Fjeldså & Krabbe 1990, Ridgely & Greenfield 2001, Hilty 2003) and refined by examining specimens of all taxa (except *A. latinuchus chugurensis* and *A. schistaceus taczanowskii*). The characters and character states appear in Appendix 3. Separately, a preliminary phylogeny of northern *Atlapetes* taxa is being constructed by J. Klicka, C. D. Cadena & J. L. Pérez-Emán through analyses of mtDNA genes cytochrome *b* and *ND2*. A sample of the *A. l. yariguierum* holotype is being analysed as part of this study and the preliminary data have been made available to us.

In the morphological study, we first analysed taxa in García-Moreno & Fjeldså's molecular phylogeny for comparative purposes, using *PAUP** v. 4.0 (Swofford 2002), with characters unordered and equally weighted, with no re-weighting. As found by García-Moreno & Fjeldså, in our strict consensus tree close relationships were observed between: (i) Black-faced Brush-finch *A. melanolaemus* and Cuzco (Sooty) Brush-finch *A. canigenis*, (ii) Yellow-breasted Brush-finches *A. latinuchus spodionotus* and *A. l. comptus*, and (iii) Slaty Brush-finches *A. s. schistaceus* and *A. s. taczanowskii*, in each case with high (>50%) bootstrap values. Conversely, Paynter (1978) hypothesised no close relationship between *A. melanolaemus* and *A. canigenis*. However, anomalously, *A. r. rufinucha* was placed in our phylogeny as more closely related to *A. latinuchus* and *A. schistaceus* taxa, and *A. tricolor* as less closely related, than García-Moreno & Fjeldså found. We recognise the limitations of a study involving so few characters (see, e.g., Kitching *et al.* 1999), especially in a group in which pigmentation can be phylogenetically less informative than in other groups. However, an analysis, encompassing a broad range of plumage characters (*cf.* Paynter 1978) can be useful, if interpreted appropriately and conservatively and will provide results comparable with future molecular studies.

Our matrix for all taxa in García-Moreno & Fjeldså's 'northern branch', as well as other Colombian and Venezuelan taxa within *A. albofrenatus*, *A. fuscoolivaceus*, *A. latinuchus*, *A. melanocephalus*, *A. schistaceus* and *A. tricolor* were subject to the same analysis. Three principal multi-taxa clades, each rooted from the same node, were identified in the strict consensus tree as follows: (i) *A. schistaceus*, subspecies *castaneifrons*, *fumidus*, *schistaceus*, *taczanowskii* and *tamae*; (ii) *A. latinuchus*,

subspecies *baroni*, *caucae*, *chugurensis*, *comptus*, *elaeoprorus*, *latinuchus*, *simplex* (=*spodionotus*), *spodionotus* and *yariguierum*; and (iii) *A. melanocephalus*, *A. latinuchus nigrifrons* and the Perijá bird. The latter grouping was supported by bootstrap (83%); the others were not. All *A. fuscoolivaceus*, *A. tricolor* and *A. albofrenatus* taxa were unresolved in our strict consensus tree at the same level. The tree is not reproduced here as we do not propose a phylogeny.

The current *A. latinuchus* complex (except *A. l. nigrifrons*, see below), including *A. l. yariguierum*, formed a monophyletic group. Preliminary data from Klicka *et al.*'s molecular analysis also suggest that *A. l. yariguierum* is most closely related to other *A. latinuchus* taxa (J. Klicka *et al. in litt.* 2005). However, this is a tentative arrangement, especially given the lack of data for other northern taxa such as *A. l. caucae*.

A lack of significant genetic divergence amongst various taxa within *A. latinuchus* (*A. l. chugurensis*, *A. l. comptus* and *A. l. spodionotus*) was noted by García-Moreno & Fjeldså (1999). We further reveal no significant intra-group differences in morphometrics (Appendix 2). Apparent intermediates between *A. l. comptus* and *A. l. spodionotus* are known from southern Ecuador and northern Peru (Ridgely & Greenfield 2001, Vellinga *et al.* 2004), suggesting a close relation between these taxa. Some morphological characters which vary within *A. latinuchus* are probably unreliable for delimiting species (Remsen & Graves 1995a). Presence or absence of a speculum is one case, having been reported as variously present and absent within the same population (Vellinga *et al.* 2004), and an apparent intergrade *A. s. tamae* / *A. s. schistaceus* (MLS 7552) had a speculum on one wing but not the other. Likewise, reported *A. l. comptus* / *A. l. spodionotus* intermediates and the surprising placement of some *A. pallidinucha* taxa in the *A. latinuchus* clade in the molecular phylogeny suggest that a paler nape is also somewhat plastic.

Our analyses point to a clear anomaly in the current sequence (the placement of *A. l. nigrifrons* within *A. latinuchus*). The position of this taxon, discussed further below, can confidently be dealt with at this time in the light of the morphological data presented herein. However, a more substantial reappraisal of the *A. latinuchus* complex would be premature in advance of Klicka *et al.*'s more comprehensive molecular analysis. We have therefore described *A. l. yariguierum* as a subspecies within the *A. latinuchus* complex. However, we strongly suspect that some taxa or groups of taxa within this complex represent species under the Biological Species Concept (Helbig *et al.* 2002) and that most of them represent species under a phylogenetic species concept (Cracraft 1983).

Before turning to the case of *A. l. nigrifrons*, its taxonomy requires comment. *A. l. nigrifrons* was described by Phelps & Gilliard (1940), but the name was subsequently changed to *A. l. phelpsi* by Paynter (1970) as the subspecific epithet was preoccupied by *A. torquatus nigrifrons*. However, with *A. torquatus* now assigned to *Buarremon* (see Hackett 1993, Remsen & Graves 1995a,b, and followed by almost all recent authors), *phelpsi* becomes a junior synonym of *nigrifrons* (Dickinson 2004).

The clade including *A. l. nigrifrons*, *A. melanocephalus* and the Perijá bird was the best supported of our northern taxa phylogeny. *A. melanocephalus* and *A. l. nigrifrons* would therefore, provisionally, appear to be more closely related to one another than either is to any of the *A. latinuchus* taxa, a proposition supported by biogeographical and morphological evidence. *A. l. nigrifrons* and *A. melanocephalus* are both restricted to the northernmost Colombian and Venezuelan mountains: the Perijá and Santa Marta ranges. Studies by Remsen & Graves (1995a) and García-Moreno & Fjeldsa (1999) suggest that some geographically close but morphologically distinctive *Atlapetes* taxa are more closely related to one another than they are to superficially similar but more geographically distant taxa. Paynter (1978) drew attention to the morphological similarity of *A. l. nigrifrons* (then *A. l. phelpsi*) and *A. melanocephalus*, which share a black forehead (with *A. melanocephalus* possessing an entirely black crown), black chin, lack of pale moustachial markings (the malar merging with the mask), distinctly greyish cheeks and a paler grey back, features not found in northern *A. latinuchus* taxa. A lineage extending from *A. a. albofrenatus* (green back; moustachial stripe; black forehead; red crown), through the Perijá bird (green back; moustachial merging with malar; black forehead; red crown) and *A. l. nigrifrons* (grey back; moustachial merging with malar; black forehead; red crown) to *A. melanocephalus* (grey back; moustachial merging with malar; black forehead; black crown), although not supported by our phylogenetic analysis, wherein *A. albofrenatus* taxa behaved counter-intuitively, appears a more plausible hypothesis than any close relation between *A. l. nigrifrons* and northern *A. latinuchus* taxa.

The assignment of *A. l. nigrifrons* to the *A. latinuchus* species-group appears to be a clear example of the current sequence failing to reflect natural groupings, per García-Moreno & Fjeldså (1995). If not assigned species rank, a better placement for *nigrifrons* is in either *A. melanocephalus* or *A. albofrenatus*. Other possible approaches, lumping *A. melanocephalus* and/or *A. albofrenatus* within *A. latinuchus*, defy rationale. Significant morphological differences exist between northern *A. latinuchus*, *A. l. nigrifrons*, *A. melanocephalus* and *A. albofrenatus*, and are considerably greater than those between various southern forms now treated specifically. Under a modernised Biological Species Concept (Helbig *et al.* 2002) and given almost certain paraphyly of *A. latinuchus*, we consider that *A. l. nigrifrons* is better treated specifically. The status of this taxon under a phylogenetic species concept should also be beyond doubt. Perijá Brush-finch is an appropriate vernacular name for *A. nigrifrons*.

Finally, it merits further consideration that *A. albofrenatus* was not monophyletic in our analysis. The close resemblance of *A. a. albofrenatus* to *A. schistaceus* was discussed previously (Remsen & Graves 1995a). In our majority rule and Adams consensus trees, *A. a. albofrenatus* grouped with the five *A. schistaceus* taxa and not *A. a. meridae*. The lack of a very close relationship between *A. a. meridae* and *A. a. albofrenatus* was further supported by morphometric data: *A. a. albofrenatus* averages larger in both wing- and tail-length than *A. a. meridae* (Appendix 2; *cf.*

Paynter (1978) who considered that 'no difference in size is apparent' between these taxa). No contact zone is known between them, *A. a. albofrenatus* being restricted to the Eastern Andes of Colombia and *A. a. meridae* to the Mérida Mountains of Venezuela. Despite morphological differences between them, we suspect that *A. a. albofrenatus* is indeed the closest extant relative of *A. a. meridae* (though the converse may not be true given the probable link between *A. a. albofrenatus*, the Perijá bird and *A. l. nigrifrons*, and possible links between *A. a. albofrenatus* and *A. schistaceus*). *A. a. albofrenatus* and *A. a. meridae* are morphologically more dissimilar (both in plumage and biometrics) than other closely related *Atlapetes* taxa now treated specifically (following García-Moreno & Fjeldså 1995). They surely represent species under a phylogenetic species concept and quite probably under the Helbig *et al.* (2002) interpretation of the Biological Species Concept. However, insufficient evidence exists to suggest that *A. albofrenatus* is paraphyletic, and an analysis of genetic and/or vocal data is lacking.

Conservation

A. l. yariguierum is endemic to the Colombian East Andes EBA (038: Stattersfield *et al.* 1998). It technically qualifies for IUCN Category D2 Vulnerable status due to its Area of Occupancy being less than 100 km^2 and being certainly known from fewer than five localities. However, if confirmed at all of the additional localities mentioned above, its status would be Near Threatened. Extensive field work in the main Cordillera in dptos. Santander and (particularly) Boyacá during the past 50 years have yielded just a handful of specimens. The taxon appears to be somewhat rare even in primary habitat. Despite specific searches, field work at the type locality produced just one capture and no observations, and, at Lepipuerto, just one sighting and no captures. At our páramo site on the east slope of the Yariguíes range, it was more common, being observed daily. Like other members of the *A. latinuchus* group (Hilty 2003), the new taxon appears to tolerate secondary habitats and may be more numerous in these than in primary forest.

Protected areas in the Eastern Andes (e.g. Parques Nacionales Naturales Pisbe, El Cocuy, Tamá, Sumapaz, Chingaza, Los Picachos, Alto Fragua, Indi-Wasi and Catatumbo) are concentrated in the highest páramos or on the east slope, and all are subject to varying levels of deforestation and human occupancy. Serranía de los Yariguíes, one of the last forest wildernesses within this Critical-rated EBA (Stattersfield *et al.* 1998), was for 24 years subject to a 'conservation plan'. Following our work and with the impetus of the Ministerio de Medio Ambiente, Corporación Autónoma Regional de Santander (CAS), various mayoralties of the region and NGOs, the Serranía de los Yariguíes National Park was finally declared on 16 May 2005. The new protected area should assist in conserving *A. l. yariguierum* and other threatened birds including Black Inca *Coeligena prunellei*, *Odontophorus strophium*, *Macroagelaius subalaris* and Saffron-headed Parrot *Pionopsitta pyrilia* (Donegan *et al.* 2005, Donegan & Huertas 2005, Huertas & Donegan 2006).

Comments on brush-finch vernacular names

García-Moreno & Fjeldså (1999) suggested the English names 'Northern Rufous-naped Brush-finch' for *A. latinuchus* and 'Bolivian Rufous-naped Brush-finch' for *A. rufinucha*. However, 'Northern Rufous-naped Brush-finch' scarcely befits *A. latinuchus*, given that at least two taxa in the group (*A. l. baroni* and *A. l. chugurensis*) have white or cream napes, and that this name incorrectly implies *A. rufinucha* to be its sister species. Further, rufous-naped is a translation of the Latin species epithet of *A. rufinucha*, not *A. latinuchus*. The name 'Cloud-forest Brush-finch' was also recently proposed (Clements & Shany 2001), but *A. latinuchus* is one of many *Atlapetes* species found in such zones and *A. l. baroni*, *A. l. caucae* and *A. l. chugurensis* are not restricted to cloud forests. Given this, J. V. Remsen *in* Dickinson (2003) proposed a third name, 'Yellow-breasted Brush-finch', which is consistent with the plumage of all group members and distinguishes it from some *Atlapetes*, but not from many others, e.g., Dusky-headed Brush-finch *A. fuscoolivaceus*, Yellow-headed Brush-finch *A. flaviceps*, Tricoloured Brush-finch *A. tricolor* or Moustached Brush-finch *A. albofrenatus*, and also has the potential to confuse with Yellow-throated Brush-finch *A. gutturalis*. 'Cloud-forest Brush-finch' and 'Northern Rufous-naped Brush-finch' were both rejected by the AOU South American Checklist Committee. None of the English names proposed to date is particularly satisfactory, reflecting the lack of unifying plumage characters for *A. latinuchus* and that the group almost certainly contains several biological and multiple phylogenetic species. 'Yellow-breasted Brush-finch', whilst not ideal, was recently adopted by the AOU South American Checklist Committee (Remsen *et al.* 2006). Doubtless a new suite of vernacular names will become necessary when *A. latinuchus* is, almost inevitably, split. The English name proposed herein for *A. l. yariguierum* is proposed only as a name for this taxon and not to any larger grouping (e.g. with *A. l. elaeoprorus* and/or *A. l. spodionotus*).

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APPENDIX 1

Specimens examined.

A. fuscoolivaceus: IAVH 7870, 11782, 11801; ICN 3169, 27333, 27336, 27370.

A. melanocephalus: NHM 1885.6.8.125, 1885.6.8.452; IAVH 558, 944, 966, 2056–2058, 2064, 2067, 2240, 3085, 11300, 11311; ICN 23504–23515, 21690; MLS 7505

A. latinuchus baroni NHM unnumbered, 1896.10.6.228, 1896.10.6.229

A. latinuchus caucae ICN 3179, 3350, 19814, 25661, 25934, 25935, 26069, 29016, 29748, 29758, 29804, ; MLS 7530, unnumbered; MNHN 2374 (NB: only Colombian *A. latinuchus* group specimens inspected in detail at MNHN).

A. latinuchus comptus NHM 1883.6.12.930, 1885.6.8.149.

A. latinuchus elaeoprorus NHM 1885.6.8.150, 1885.6.12.931; IAVH 2263, 2310, 11699; ICN 20169, 34701; MLS 7528, 7530, 7870; MNHN 2375, 3754.

A. l. latinuchus NHM 1885.6.12.926, 1896.10.6.230–1896.10.10.233, 1900.10.2.93, 1924.2.14.22, 1924.2.14.23, 1953.68.464.

A. [*latinuchus*] *nigrifrons* ICN 32692; COP (photo) 55881, 55882, 55890, 55900, 55902, 55905, 58251, 73053, 73323, 73326, 73333, 73337; ICN 32646 ('Perijá bird').

'*A. latinuchus simplex*' (= *A. l. spodionotus*) NHM 1893.12.12.18.

A. latinuchus spodionotus NHM 1860.11.9.9, 1860.11.20.83, 1885.6.147, 1885.6.8.148, 1885.6.12.928, 1885.6.12.929, 1900.10.2.87, 1900.10.2.88, 1925.12.24.283, 1925.12.24.284, 1938.12.20.122, 1940.12.5.117–1940.12.5.120, 1940.12.5.214, 1940.12.5.960, 1940.12.5.961, 1969.52.520, 1969.52.521, 1977.5.7–1977.5.11; UMZC 27/Fri(E)/8/r/1–27/Fri(E)/8/r/4; ICN-UN 33355; MLS 7531, 7532, MNHN 2376.

A. latinuchus yariguierum ICN 3199, 10322, 25111, 34016 (holotype); UIS 1412; FMNH (photo) 220606, 220607.

A. a. albofrenatus NHM 1885.6.8.152, 1885.6.8.153, 1885.6.12.932, 1885.6.12.933, 1916.9.21.141; IAVH 612, 6543, 10301, 11678, 12551; MLS 7533–7536; ICN 3171–3177, 3560, 3701, 3706, 3721, 3974, 4217, 4819, 4820, 5068, 10323, 14712, 15938, 16250, 16358, 18847, 25280, 25497, 28356, 28357, 18846, 18848, 31126, 34982; UIS 1433.

A. albofrenatus meridae NHM 90.5.15.1, 1914.11.26.673-1914.11.26.676, 1914.11.26.680, 1969.39.77, 1969.39.76, 1969.52.519.

A. schistaceus castaneifrons NHM 12.18.070, 12.204.94, 85.6.8.160, 85.6.8.161, 85.6.12.941, 1914.11.26.484, 1914.11.26.67, 1914.11.26.679, 1914.41.26.680–1914.11.26.683, 1914.11.26.685–1914.11.26.687, 1915.3.1.177, 1915.3.1.678, 1969.39.78–1969.39.80.

A. schistaceus fumidus ICN 4851, 4852.

A. s. schistaceus NHM 1845.5.24.30, 1854.1.25.100, 1857.11.28.59, 1885.6.8.156–1885.6.8.159, 1885.6.8.162, 1885.6.12.934, 1885.6.12.935, 1885.6.12.938, 1898.12.14.654–98.12.14.657, 1916.9.21.94, 1916.9.21.95, 1946.49.696, 2002.3.1044–1946.49.698; UMZC 27/Fri(E)/8/5/1–27/Fri(E)/8/5/3; IAVH unnumbered (2), 5387, 6714, 7257, 7260, 7267, 11845, 12287, 12627, 12646; MLS 7546–7548, 7550, 7551, 7553, 8245; ICN 4296–4302, 4304–4306, 4840, 4849, 4855–4864, 4866–4869, 4871–4884, 14655, 19015, 20010–20013, 20446, 22330–22332, 26220, 26234, 33709, 35012, 437125.

A. schistaceus tamae IAVH 10628, 10632, 10643, 10652, 12102, 12105; MLS 7537–7545; ICN 4853, 4854, 10681, 33936; UIS 1252.

A. canigenis NHM 1939.1.30.1.

A. r. rufinucha NHM 1846.9.9.99, 1846.99.136, 1885.4.8.144, 1885.6.8.142, 1885.6.8.143, 1885.6.8.148, 85.6.12.922–1885.6.12.924, 1902.313.334.
A. melanolaemus NHM 1902.3.13.335–1902.3.13.339.

APPENDIX 2

Biometrics of *Atlapetes* taxa.

Taxon	Sex	Wing	Tail	Tarsus	Bill	Mass
A. fuscoolivaceus	all	74.0 ± 3.4 (7)	78.4 ± 4.9 (7)	26.6 ± 0.7 (6)	16.4 ± 0.6 (5)	32.5 ± 1.5 (2)
	males	75.6 ± 2.1 (5)	80.0 ± 5.5 (5)	26.8 ± 0.9 (4)	16.7 ± 0.8 (3)	32.5 ± 1.5 (2)
	females	67.0 ± 0.0 (1)	73.0 ± 0.0 (1)	26.0 ± 0.0 (1)	16.0 ± 0.0 (1)	
A. melanocephalus	all	72.2 ± 3.5 (26)	74.0 ± 3.2 (24)	26.1 ± 1.0 (27)	16.0 ± 0.6 (24)	25.0 ± 2.8 (6)
	males	72.8 ± 4.5 (10)	76.0 ± 3.5 (10)	26.2 ± 1.1 (10)	15.9 ± 0.5 (8)	23.8 ± 2.5 (2)
	females	71.3 ± 2.4 (12)	72.2 ± 2.2 (11)	26.1 ± 0.8 (12)	16.0 ± 0.7 (12)	25.8 ± 3.75 (3)
A. latinuchus baroni	all	73.0 ± 0.0 (3)	76.7 ± 2.5 (3)	28.0 ± 0.5 (3)	15.5 ± 0.0 (3)	
	males	73.0 ± 0.0 (1)	79.0 ± 0.0 (1)	28.5 ± 0.0 (1)	15.5 ± 0.0 (1)	
	females	73.0 ± 0.0 (2)	75.5 ± 2.1 (2)	27.8 ± 0.4 (2)	15.5 ± 0.0 (2)	
A. latinuchus caucae	all	71.5 ± 2.1 (12)	72.3 ± 2.7 (12)	26.4 ± 1.1 (12)	15.3 ± 0.8 (11)	
	males	72.2 ± 2.4 (5)	73.6 ± 2.7 (5)	26.2 ± 1.5 (5)	15.4 ± 0.9 (5)	
	females	71.0 ± 1.9 (7)	71.3 ± 2.4 (7)	26.5 ± 0.8 (7)	15.2 ± 0.7 (6)	
A. latinuchus comptus	all	74.0 ± 1.4 (2)	74.5 ± 0.7 (2)	27.5 ± 0.7 (2)	15.5 ± 0.0 (2)	
A. latinuchus elaeoprorus	all	75.9 ± 3.7 (10)	73.7 ± 4.4 (11)	27.1 ± 0.7 (11)	15.9 ± 0.5 (12)	27.5 ± 0.0 (1)
	males	75.5 ± 3.5 (2)	74.5 ± 2.1 (2)	27.0 ± 0.0 (3)	16.2 ± 0.3 (3)	27.5 ± 0.0 (1)
	females	72.5 ± 4.9 (2)	69.0 ± 2.8 (2)	26.5 ± 0.7 (2)	16.0 ± 0.7 (2)	
A. l. latinuchus	all	72.6 ± 3.5 (9)	71.1 ± 3.4 (9)	26.0 ± 0.9 (8)	15.6 ± 0.4 (8)	
	males	73.8 ± 4.1 (5)	73.2 ± 2.8 (5)	26.3 ± 1.0 (5)	15.6 ± 0.5 (4)	
	females	71.0 ± 2.0 (3)	68.5 ± 2.1 (3)	25.5 ± 0.5 (3)	15.6 ± 0.3 (4)	
A. latinuchus nigrifrons	all	69.6 ± 3.3 (15)	71.0 ± 3.6 (15)	25.5 ± 0.0 (1)	15.9 ± 0.5 (3)	31.0 ± 0.0 (1)
	males	70.3 ± 4.1 (6)	73.7 ± 3.8 (6)			
	females	68.9 ± 2.7 (9)	69.7 ±2.2 (9)	25.5 ± 0.0 (1)	16.0 ± 0.0 (1)	
'Perijá bird'	all	72.0 ± 1.4 (2)	76.3 ±1.8 (2)	26.0 ± 0.0 (1)	15.3 ± 1.0 (2)	28.5 ± 0.7(2)
	females	73.0 ± 0.0 (1)	77.5 ±0.0 (1)	26.0 ± 0.0 (1)	16.0 ± 0.0 (1)	29.0 ± 0.0(1)
'*A. latinuchus simplex*'	all (=male)	78.0 ± 0.0 (1)	77.0 ± 0.0 (1)	27.0 ± 0.0 (1)	(broken)	
A. latinuchus spodionotus	all	75.9 ± 3.4 (29)	75.2 ± 5.1 (28)	26.9 ± 1.1 (28)	15.7 ± 0.5 (28)	
	males	76.4 ± 3.4 (17)	76.3 ± 5.2 (17)	26.7 ± 1.1 (18)	15.6 ± 0.5 (18)	
	females	74.9 ± 4.3 (7)	73.9 ± 5.7 (7)	27.4 ± 0.5 (6)	16.0 ± 0.4 (5)	
A. latinuchus yariguierum	all	75.3 ± 2.1 (3)	78.3 ± 1.5 (3)	27.0 ± 1.7 (3)	16.0 ± 0.0 (3)	22.6 ± 0.0 (1)
	males	77 ± 0.0 (1)	80 ± 0.0 (1)	25.0 ± 0.0 (1)	16.0 ± 0.0 (1)	22.6 ± 0.0 (1)
	females	76 ± 0.0 (1)		78± 0.0 (1)	28.0 ± 0.0 (1)	16.0 ± 0.0 (1)
A. a. albofrenatus	all	72.9 ± 2.4 (36)	73.9 ± 3.5 (37)	26.2 ± 1.0 (36)	15.9 ± 0.5 (36)	30.0 ± 2.6 (6)
	males	74.2 ± 2.6 (17)	75.2 ± 2.9 (18)	26.1 ± 1.1 (18)	16.0 ± 0.6 (18)	29.0 ± 1.2 (4)
	females	71.8 ± 1.6 (10)	72.6 ± 3.0 (10)	25.8 ± 0.8 (9)	15.9 ± 0.5 (10)	32.0 ± 4.2 (2)
A. albofrenatus meridae	all	67.2 ± 2.4 (9)	68.0 ± 2.9 (9)	26.5 ± 1.2 (8)	15.7 ± 0.7 (9)	
	males	68.0 ± 1.7 (3)	69.0 ± 1.0 (3)	26.7 ± 0.8 (3)	15.7 ± 0.3 (3)	
	females	63.0 ± 0.0 (1)	65 ± 0.0 (1)	25.0 ± 0.0 (1)	16.5 ± 0.0 (1)	
A. schistaceus castaneifrons	all	70.5 ± 3.0 (18)	73.0 ± 4.2 (18)	27.3 ± 1.0 (18)	15.7 ± 0.5 (17)	
	males	70.9 ± 3.0 (13)	73.7 ± 4.3 (13)	27.4 ± 0.8 (13)	15.8 ± 0.5 (12)	
	females	69.3 ± 4.0 (3)	71.3 ± 3.1 (3)	27.9 ± 0.8 (3)	15.7 ± 0.8 (3)	
A. schistaceus fumidus	all	72.5 ± 3.5 (2)	72.5 ± 2.1 (2)	27.3 ± 0.4 (2)	15.8 ± 0.4 (2)	
	males	75.0 ± 0.0 (1)	74.0 ± 0.0 (1)	27.5 ± 0.0 (1)	16.0 ± 0.0 (1)	
	females	70.0 ± 0.0 (1)	71.0 ± 0.0 (1)	27.0 ± 0.0 (1)	15.5 ± 0.0 (1)	
A. s. schistaceus	all	75.5 ± 3.3 (81)	77.5 ± 4.5 (82)	26.8 ± 0.9 (83)	15.0 ± 0.6 (81)	28.2 ± 2.6 (11)
	males	78.0 ± 2.2 (26)	80.3 ± 3.0 (25)	27.0 ± 0.7 (25)	15.0 ± 0.5 (23)	28.5 ± 1.3 (4)
	females	74.3 ± 2.6 (28)	76.4 ± 3.4 (27)	26.7 ± 0.8 (29)	15.2 ± 0.7 (30)	
A. s. schistaceus	all	76.1 ± 3.1 (46)	78.7 ± 3.7 (45)	26.8 ± 0.8 (48)	15.1 ± 0.5 (46)	28.0 ± 3.0 (8)
Eastern Andes	males	78.0 ± 2.2 (20)	80.2 ± 3.2 (19)	27.0 ± 0.8 (20)	15.0 ± 0.5 (18)	28.0 ± 1.0 (3)

	females	74.6 ± 2.4 (19)	76.7 ± 2.9 (18)	26.5 ± 0.6 (20)	15.2 ± 0.7 (21)	27.8 ± 5.5 (3)
A. s. schistaceus	all	77.0 ± 2.5 (12)	79.4 ± 3.1 (12)	26.7 ± 0.9 (10)	15.2 ± 0.7 (10)	28.8 ± 1.0 (3)
Western and Central Andes	males	78.6 ± 2.5 (5)	81.3 ± 2.9 (5)	27.0 ± 0.4 (4)	15.1 ± 0.8 (4)	30.0 ± 0.0 (1)
	females	75.0 ± 2.0 (3)	78.7 ± 3.5 (3)	25.8 ± 1.2 (3)	15.0 ± 1.0 (3)	
A. schistaceus tamae	all	74.5 ± 2.9 (17)	74.8 ± 3.0 (18)	27.4 ± 0.8 (18)	15.7 ± 0.6 (15)	26.4 ± 1.5 (7)
	males	75.9 ± 2.0 (9)	76.0 ± 2.0 (10)	27.4 ± 0.6 (10)	15.8 ± 0.5 (9)	27.3 ± 1.5 (4)
	females	73.8 ± 4.2 (4)	72.8 ± 4.6 (4)	27.5 ± 1.1 (4)	15.5 ± 0.5 (3)	26.0 ± 0.0 (1)
A. canigenis	unknown	69.0 ± 0.0 (1)	68.0 ± 0.0 (1)	27.5 ± 0.0 (1)	17.0 ± 0.0 (1)	
A. r. rufinucha	all	69.1 ± 4.1 (10)	64.6 ± 4.4 (10)	25.9 ± 1.0 (10)	15.0 ± 0.7 (10)	
	females	68 ± 0.0 (1)	62 ± 0.0 (1)	25 ± 0.0 (1)	14.0 ± 0.0 (1)	
A. melanolaemus	all	68.8 ± 2.9 (6)	67.8 ± 3.8 (6)	27.2 ± 0.5 (6)	15.0 ± 0.7 (6)	
	males	71.5 ± 2.1 (2)	71.0 ± 4.2 (2)	27.3 ± 0.4 (2)	15.0 ± 1.4 (2)	
	females	67.0 ± 2.6 (3)	65.7 ± 3.1 (3)	27.2 ± 0.8 (3)	15.0 ± 0.5 (3)	

APPENDIX 3

Matrix of characters and description of characters used in phylogenetic analysis

Taxon | Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
B. brunneinucha (outgroup)	2	0	0	2	0	0	1	2	0	4	0	1	1	1	0	1
A. fuscoolivaceus	1	0	2	1	0	0	1	0	0	4	0	0	0	0	1	1
A. t. tricolor	1	0	1	2	0	0	1	0	0	4	0	0	0	0	1	1
A. tricolor crassus	1	0	1	2	0	0	1	0	0	4	0	0	1	0	1	1
A. melanocephalus	1	0	2	0	0	0	0	2	1	0	2	0	0	0	2	0
Perijá bird	1	0	0	2	0	0	0	2	0	0	1	0	0	0	0	0
A. latinuchus baroni	1	1	0	0	0	1	1	0	0	2	0	0	0	0	0	1
A. latinuchus caucae	1	0	0	0	1	1	1	0	0	3	0	0	0	0	0	1
A. latinuchus chugurensis	1	1	0	0	0	1	1	0	0	3	0	0	0	0	0	1
A. latinuchus comptus	1	1	0	0	0	2	1	0	0	2	0	0	0	0	0	1
A. latinuchus elaeoprorus	1	0	0	0	1	1	1	0	0	3	0	0	0	0	0	1
A. l. latinuchus	1	0	0	0	1	1	1	0	0	2	0	0	0	0	0	1
A. latinuchus nigrifrons	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0
A. latinuchus simplex	1	0	0	0	0	1	1	0	0	3	0	0	0	0	0	1
A. latinuchus spodionotus	1	0	0	0	0	1	1	0	0	3	0	0	0	0	0	1
A. latinuchus yariguierum	1	0	0	0	0	0	1	0	0	3	0	0	0	0	0	1
A. a. albofrenatus	1	0	0	2	0	0	1	1	0	0	0	0	0	0	1	1
A. albofrenatus meridae	1	0	0	2	0	0	1	2	0	2	0	0	0	0	0	1
A. schistaceus castaneifrons	0	0	0	0	0	1	1	0	0	0	0	0	?	0	1	1
A. schistaceus fumidus	0	0	0	0	0	1	1	0	0	0	0	0	?	0	1	1
A. s. schistaceus	0	0	0	0	1	2	1	1	0	0	0	0	?	0	1	1
A. schistaceus taczanowskii	0	0	0	0	0	2	1	1	0	0	0	0	?	0	1	1
A. schistaceus tamae	0	0	0	0	0	0	1	1	0	0	0	0	?	0	1	1
A. canigenis	0	0	0	0	0	0	1	1	1	?	0	0	?	0	0	1
A. r. carrikeri	1	0	0	1	0	0	1	1	0	1	0	0	1	0	0	1
A. r. rufinucha	1	0	0	0	0	2	1	1	0	1	0	0	1	0	0	1
A. melanolaemus	1	0	0	0	0	0	0	1	1	?	0	0	1	0	2	0

Matrix of plumage characters. 1. Belly (0=grey, 1=yellow, 2=white); 2. Pale nape (0=absence, 1=presence); 3. Crown (0=rufous, 1=tawny/yellowish, 2=neither rufous nor tawny); 4. Olivaceous on back (0=none, 1=tinge, 2=deep olive / green); 5. Visible speculum (0=absence, 1=presence); 6. Supraloral spot (0=none/vestigial, 1=small, 2=large); 7. Chin (0=black, 1=as breast or whiter); 8. Forehead (0=rufous/tawny, 1=narrow black, 2=broad black); 9. Mottling on breast (0=absence, 1=presence); 10. Dark malar (0=thick, 1=strong, 2=moderate, 3=faint, 4=none); 11. Cheeks (0=black/as mask, 1=dark grey, 2=pale grey); 12. Breast-band (0=absence, 1=presence); 13. Melanism of flanks (0=light, 1=strong); 14. Orange supercilium (0=absence, 1=presence); 15. Throat and upper breast (0=homogeneous with belly, 1=distinctly lighter, 2=distinctly darker); 16. Paler moustachial region (0=absent, 1=present).